SHORT COMMUNICATION

Emerging tree diseases are accumulating rapidly in the native and non-native ranges of Holarctic trees

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Abstract

Emerging infectious diseases threaten natural and managed trees worldwide – causing reduced vigour, increased mortality and, occasionally, extirpation – yet we have little understanding of how emerging diseases have accumulated over time and how accumulation has varied by host species, host nativity and in different global regions. To address this challenge, I assembled over 900 new disease reports on 284 tree species in 88 countries and quantified how emerging infectious diseases have accumulated geographically and on different hosts. I show disease accumulation is increasing rapidly globally, with numerous recent years having nearly twice the number of new records as the twenty-year average and the number of new reports doubling every ~ 11 years. Of the tree genera assessed, *Pinus* had by far the most new diseases reported over the last several decades, likely reflecting both its large native range in the Northern Hemisphere and its wide use in forestry globally. Most hosts tend to accumulate more diseases in their native ranges than their non-native ranges, consistent with pathogen introductions causing most new diseases. Europe and Central Asia had the most accumulated emerging diseases, but accumulation is also increasing rapidly in East Asia. This work suggests that the impacts of emergent tree diseases are likely to continue to compound in the future and threaten native and planted forests worldwide.

Keywords

emerging infectious diseases, global trends, host jumps, non-native plants, plant pathogens, pathogen accumulation

Introduction

Emerging infectious diseases (EIDs) – defined as diseases that have, in the past several decades, expanded their host breadth, geographic range, increased in severity or are newly discovered, recognized or re-emerged (Anderson et al. 2004; Ghelardini et al.

2016) – are a threat to natural and managed plants. Particularly damaging EIDs over the past decades have threatened native plant populations with expiration (Anderson et al. 2004) and have reduced the yield and vigour of non-native plants cultivated for aesthetics, agriculture or forestry (Ristaino et al. 2021). Impacts on host populations have resulted in numerous EIDs reshaping forests around the globe. Perhaps the most well-known tree disease in North America, chestnut blight (caused by *Cryphonectria parasitica*) effectively eliminated chestnut as an overstorey tree in its native range in the Appalachian Mountains and facilitated a transition to oak/hickory dominated forests (McCormick and Platt 1980). Although most EIDs do not have such dramatic effects on their hosts, the continued emergence of new diseases increases the likelihood of particularly damaging diseases emerging, reducing host populations and shifting forest community composition. Ash dieback in Europe, Jarrah dieback in Australia and *Torreya* mycosis in Florida, for instance, are each causing similar host population declines that may result in host extirpation and co-extinction of associated species.

Increased global trade and connectivity and shifting environmental conditions have facilitated the emergence of many infectious diseases, with most EIDs being due to introductions and weather events (Anderson et al. 2004). EIDs due to introductions frequently cause small effects on hosts in their native ranges, likely due to long-term co-evolutionary history, but when exposed to novel hosts – often closely related to those in their native ranges – can cause mortality previously unseen in the native range (Loo 2009) as hosts may lack any evolved resistance to the pathogen (Ghelardini et al. 2017). Other pathogens can emerge from shifting biotic or climatic regimes, that may increase the likelihood of spread and establishment. Climate change can both create more favourable conditions for pathogens and stress host plants that, together, can facilitate attack by pathogens. As climates shift away from their historic norms, hosts and pathogens may need to shift their geographic ranges and the balance of their interactions may similarly shift (Corredor-Moreno and Saunders 2020). Warmer winters, greater precipitation and higher humidity may each act to, generally, improve conditions for pathogens, while high heat and drought may stress host plants making them less able to resist infection. Recent climate shifts, for instance, have likely increased the prevalence of *Cronartium ribicola* in portions of western United States and facilitated its spread to previously inhospitable areas (Dudney et al. 2021). Likewise, the increased frequency of climate-linked extreme events (Rahmstorf and Coumou 2011) also have the potential to increase the rate of EIDs (Rosenzweig et al. 2001), by creating unique conditions conducive to tree stress and favourable to pathogen populations. Numerous tree EID outbreaks have been linked to climate change or are predicted to be impacted by future climate change (e.g. Woods et al. 2005; Aguayo et al. 2014; Goberville et al. 2016; Kolb et al. 2016; Contreras-Cornejo et al. 2023), suggesting the possibility of even more damaging EIDs in the future.

Changing biotic communities have also facilitated the emergence of EIDs. Many pathogen and insect pest species have been known to track their hosts to new regions, which may then spill over to new hosts. Bonnamour et al. (2023), for instance, recently showed that non-native plant introductions have frequently preceded insect introduc-

tions, suggesting that non-native plant accumulation likely contributes in concert to pathogen spread and accumulation in new regions outside their historic ranges. Further, many pathogens are only known to affect their tree hosts outside their hosts' native ranges (Gougherty and Davies 2022b), which may then be transported back to the native range where it may damage native populations. Non-native trees offer a useful bellwether for identifying future pest threats before they have the opportunity to arrive in a host's native range. For instance, in a review of the fungal pathogens of European and Eurasian trees grown in Siberia, Tomoshevich et al. (2013) identified dozens of previously unknown fungal-host associations, a substantial portion of which were considered "high impact," that could threaten tree populations if transported back to tree's native ranges.

While much is known about the spread and emergence of some individual, particularly high impact, EIDs (e.g. Grünwald et al. 2012; Bulman et al. 2016; Burgess et al. 2017; Enderle et al. 2019; van der Nest et al. 2019; Futai 2021), less is known about the overall, general temporal trends of EID accumulation and how these trends vary by geographic regions, host species and host nativity. Understanding where and which hosts are most likely to accumulate pathogens can be important for future surveillance and management, especially as eradication often becomes unfeasible after pathogens begin to spread on the landscape (Smith et al. 2017). To address this challenge, I compiled hundreds of reports of EIDs on new tree hosts and in new geographic regions and compared the accumulation of EIDs in different global regions and in locations where hosts are native and non-native. I focused on a set of widely distributed tree genera, mostly native to the Holarctic, with large native and non-native ranges, that have been introduced (intentionally and not) to many different regions of the world. The "big data" approach used in this study helps to characterise the growing threat posed by EIDs and how this threat is unequally distributed regionally and by host species.

Methods

Literature search and data extraction

To find relevant reports of new EIDs, I searched the primary literature using multiple databases. Searches primarily involved identifying records where pathogens were identified on new hosts, new geographic regions or were reported to be increasing in severity. The plant pathology literature has a history of reporting such records as "First reports" which typically involve researchers describing the location, host and symptoms of the disease and the approach used to verify the pathogen. This often involves validating Koch's postulates (an established approach to demonstrate a causal link between a disease and suspected pathogenic microorganisms) for fungi, bacteria and nematodes, performing molecular techniques for viruses and phytoplasmas and morphological verification for parasitic plants. These new results are often published with titles such as "First report of [pathogen] causing [disease] on [host] in [locale]."

I used several approaches to find relevant reports of recent EIDs. First, I searched multiple online databases for "first report", "first record", "first occurrence", "newly reported", "for the first time" and "first finding". Searches were primarily conducted with PubAg and PubMed and Wiley Publishers for a select number of publication titles not included in PubAg. PubAg is a public catalogue of agriculture-related publications and was accessed by the PubAg API (https://pubag.nal.usda.gov/apidocs) with R statistical software (v.4.2.0). Searches involved querying article titles in seventeen plant-based journals including "Archiv für Phytopathologie und Pflanzenschutz", "Australasian plant disease notes", "Australasian plant pathology", "Bulletin OEPP", "Canadian Journal of plant pathology", "Crop protection", "European Journal of plant pathology", "Forest pathology", "Journal of general plant pathology", "Journal of plant pathology", "Microbial pathogenesis", "Phytoparasitica", "Phytopathologische Zeitschrift", "Plant disease", "Plant health progress", "Plant pathology" and "Plant Protection Science." Searches were limited to the years 2000 to 2022 to align with the temporal definition of emerging diseases and to capture the most recent EIDs. Although records from 2022 may be incomplete, as the final search was conducted in January 2023, these records were, nevertheless, included as they represent the most recently-confirmed EIDs. Any reports currently listed as a "First look", before publication in a journal issue, were assigned to 2022.

Next, I searched CAB Direct for the same terms as those above (i.e. "first report", "first record" etc.). CAB Direct is a unique resource as it indexes scientific publications, reports and conference abstracts (many of which, CABI states, are unavailable elsewhere) published in over a hundred countries and over 80 languages. Finally, I manually searched the table of contents of "Plant Disease" – Disease Notes, "New Disease Reports", "Forest Pathology" and "Plant Pathology" for relevant records. Although I attempted to be comprehensive in these searches by using multiple search terms and multiple unique databases, it is likely that some relevant EID reports were unintentionally omitted.

As this work was focused on tree species and, in particular, species that have extensive native and non-native ranges, I focused on a select number of species-rich host tree genera mostly native to the Holarctic, including *Abies, Acacia, Acer, Alnus, Betula, Carya, Castanea, Eucalyptus, Fagus, Fraxinus, Juglans, Larix, Picea, Pinus, Platanus, Populus, Pseudotsuga, Quercus, Robinia, Tectona, Thuja, Tilia, Tsuga* and *Ulmus*. Genera mostly from the Holarctic were selected because: (i) higher latitude species tend to have larger geographic ranges than low latitude species (i.e. Rapoport's rule) – thus, they many exist as natives or non-native in many regions, (ii) these genera represent some of the most widely grown species for forestry and cultivation and occasionally act as invasives and (iii) European (Lenzner et al. 2022) and North American colonialism have spread native trees of these regions to many other parts of the Globe, increasing the likelihood they may be exposed to new pathogens. Other genera (e.g. *Eucalyptus, Acacia*) were included because they tend to be widely planted for forestry.

After searching for all new disease reports, titles were searched for the common and scientific names of the tree genera listed above. Any record that matched was retained

for further analysis. Next, to partially automate the data gathering process, titles were searched for country names and pathogen names. I used the country-code package in R statistical software (v.4.2.0) (Arel-Bundock et al. 2018) for standardised country names and regional affiliations (based on World Bank Development Indicators regions). Pathogen names were downloaded from the CABI Crop Protection Compendium (CABI 2023), which maintains datasheets on > 10,000 plant pests with contemporary names. Records that did not have a matching country name or pathogen name were retained regardless and all records were checked manually to ensure the extracted host, pathogen and country names were accurate. Duplicate records from the same country were removed, with only the earliest record being retained. Thus, the retained records considered spread between countries, but not spread within countries unless, while spreading within a country, the pathogen became associated with a new host.

Host nativity assignment

Host nativity was determined using the GlobalTreeSearch (GTS; https://tools.bgci.org/global_tree_search.php), which maintains checklists of native trees for nearly all countries (Beech et al. 2017). For each country-host occurrence in the dataset, hosts were considered native in a focal country if: (i) the species was included in the GTS and (ii) the species was included in the checklist for the focal country. This two-step process was necessary as some hosts were not included in the GTS (e.g. because they were synonyms, hybrids or not distinguished below the genus-level). Any host species not included in the GTS were checked manually. In some instances, where hosts were only identified to the genus-level, they were considered non-native if no species of the genus occurred natively in the country (e.g. *Eucalyptus* hybrids outside Australasia). Otherwise, the nativity was left ambiguous and not included in any native/non-native comparisons. Hybrids followed a similar rule – if both parent species were known to be native to a country, the hybrid was considered native. If neither parent species was native, it was considered non-native and nativity was left ambiguous if one parent species was native and the other was not. In total, only a small percentage (3.8%) of hosts in the dataset were found to have ambiguous origins. All species names (both in the EID reports and GTS) were standardised to the Global Biodiversity Information Facility (GBIF) taxonomic backbone, using the rgbif package (Chamberlain and Boettiger 2017), before matching. The complete dataset is available in Suppl. material 2.

Analyses

I assessed the temporal accumulation of EIDs globally and separately for multiple geographic regions and host genera. Accumulation was calculated simply as the cumulative sum of new reports published since 2000. While I acknowledge publication may occur several years after sampling, which may itself be several years after the disease initially emerged, publication year was the only consistently reported time-stamp and represents the time the information became widely available. Exponential models

were fitted to accumulation curves to visualise increasing accumulation (concave up-wards) versus saturation (concave downwards). An exponential model was chosen as the rate of new reports is expected to change over time, contingent on host species and geographic region and whether new reports are increasing or declining. Compared to a linear model, an exponential model should be able to capture the changing rate of accumulation over time. Models were fitted with the nls function in the stats package (R Core Team 2023), as $y \sim a \times \exp(b \times x) + c$, where y is the cumulative number of new reports and x is the number of years elapsed since 2000 (the first year of data collection). To facilitate interpretation and visualisation, in the below plots, x was back-transformed to year (by adding 2000). Model fit was estimated by pseudo R^2, calculated from the aomisc package (Onofri 2020). Approximate doubling time of new reports was calculated by fitting a logarithmic model: $\log_2(\text{new reports}) \sim \text{year} + \text{intercept}$ and calculating the inverse of the slope estimate.

As most countries and tree genera have more native than non-native tree species, the accumulation curves and models were also plotted after standardising the cumulative sum by the number of native and non-native species. These plots and analyses thus represent the number of EID reports per species, thereby controlling for the unequal frequency of native and non-native species.

In addition to quantifying the temporal accumulation of EID reports, I also assessed the relationship between the number of EID reports and the accumulated number of total agricultural and biological documents published in literature, extracted from Scimago Journal & Country Rank (SCImago 2022) from 2000 to 2021. This analysis helped reveal how EID reports have increased with increased sampling and documentations, as represented by the number of citable scientific documents.

Results

In total, 962 host-pathogen-location EIDs were identified, from 2000 onwards, across 24 host genera (including > 280 species) and 88 countries. Globally, reports of EIDs have increased rapidly over time (Fig. 1) and in proportion with the expanding agricultural and biological literature (Suppl. material 1: fig. S1). New reports of EIDs on the focal genera, however, have not increased relative to the total number of new EID reports for all host species (i.e. including crops and other non-tree species) (Suppl. material 1: fig. S2). A median of 42 new EIDs were reported annually on trees of the 24 focal genera although 2019 had twice that number. The increase is seen both in regions where hosts are native and non-native although, to date, countries where species are native have accumulated more pathogens. Doubling time for new EID reports was approximately 11.2 years for all hosts, but 14.3 years for native hosts and 8.7 years for non-native hosts.

Interestingly, the patterns of accumulation differed by region (Fig. 2). Total accumulation was highest in Europe, both amongst native and non-native trees. This is likely due to a combination of increasing importation of non-native pathogens (Santini et al. 2013), well-developed international reporting systems (e.g. European Plant

(a)

(b)
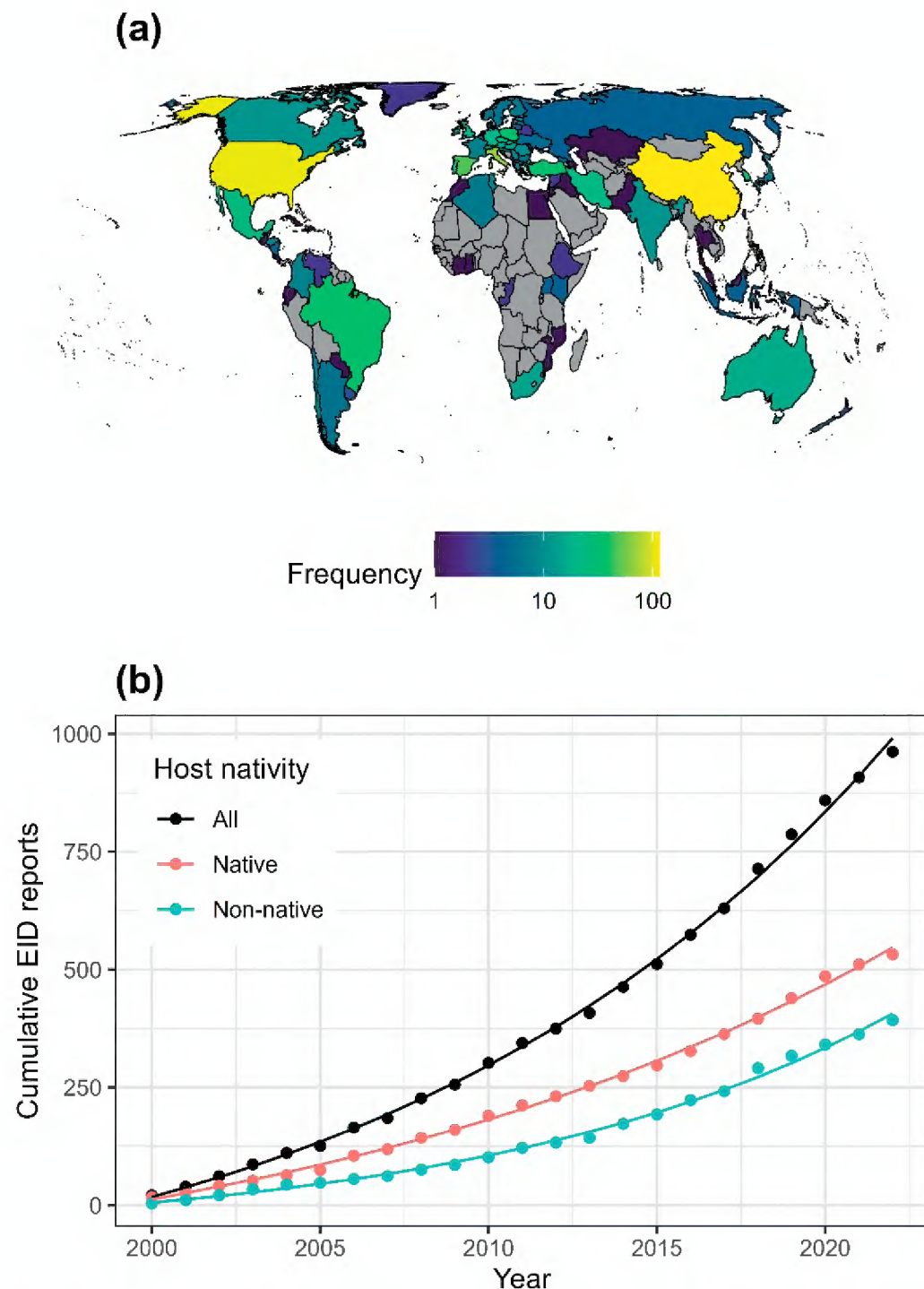
Figure 1. a geographic distribution and **b** temporal accumulation of 962 first reports of tree EIDs since 2000 for 24 tree genera. Note the scale in (**a**) has been $\log_{10}$ transformed and no reports of EIDs were found for countries coloured grey. Models in (**b**) were fitted as $y \sim a \times \exp(b \times x) + c$, where y is the cumulative number of new reports and x is the number of years elapsed since 2000 (the first year of data collection). To facilitate interpretation and visualisation, x was back-transformed to year (by adding 2000). Native and non-native reports in (b) do not always sum to the total, as numerous host species had ambiguous geographic origins.

Protection Organisation) and relatively small country sizes – where a pathogen may be considered 'new' even if it has been reported in an adjacent region (but different country). North America has similarly seen increasing pathogen accumulation, but growth is considerably slower in both native and non-native trees. Parameter estimates suggest accumulation is saturating in North America for non-native trees (Suppl. material 3). This slower accumulation could be due to relatively large country sizes (i.e. United States and Canada) – although many first reports for the US and Canada are at
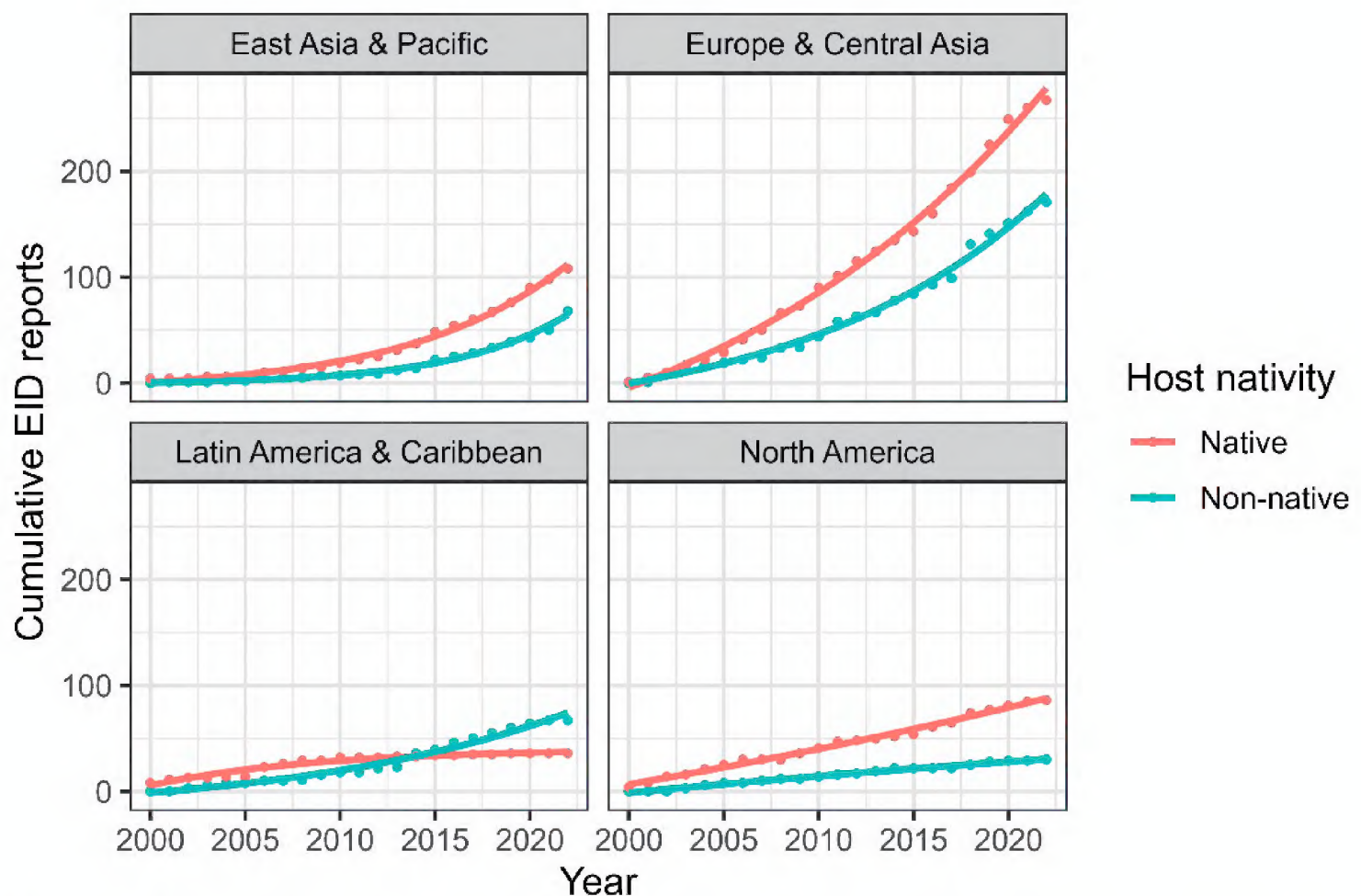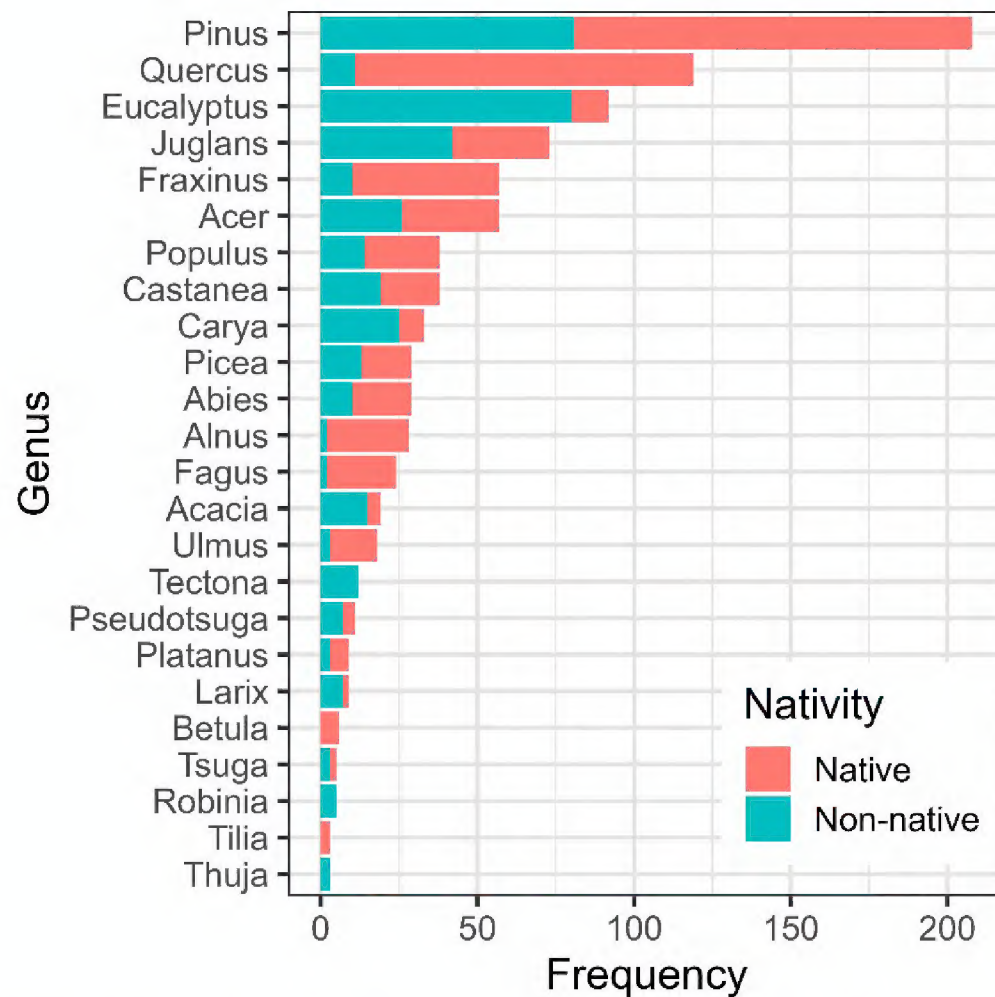
Figure 2. Temporal accumulation of first reports of tree EIDs since 2000 for four geographic regions and 24 tree genera. Models were fitted as y ~ a × exp(b × x) + c, where y is the cumulative number of new reports and x is the number of years elapsed since 2000 (the first year of data collection). To facilitate interpretation and visualisation, x was back-transformed to year (by adding 2000). See also Suppl. material 1: fig. S3.

the state/province level – but also effective pathogen/pest exclusion policies (e.g. Plant Quarantine Act of 1912; Plant Protection Act of 2000).

Pathogen accumulation on native and non-native trees in East Asia were similar to those in North America and Europe, but seemed to be increasing at a more rapid pace, perhaps due to increased introductions of non-native pathogens and improved reporting. Not surprisingly, accumulation of pathogens on natives in Latin America and Caribbean was slow and tended towards saturation (Suppl. material 3), as most of the genera investigated here were not native to this region. However, like East Asia, the accumulation on non-native plants is increasing rapidly, perhaps due to increased planting of non-native trees for forestry in this region. When standardised by the total number of native and non-native species, accumulation trends were similar in each global region, but the native and non-native curves for North America and East Asia and Pacific were nearly identical – indicating that EID accumulation per species, is similar for native and non-native trees in these regions (Suppl. material 1: fig. S3).

EID accumulation varied substantially amongst the genera assessed (Fig. 3), but like the regional patterns, accumulation was frequently higher in species' native, rather than non-native ranges (Fig. 4). *Pinus* provides a clear example of reports of new pathogens tending to be higher in the native region. Notably, however, when standardised by the total number of native and non-native species, the accumulation trends have

Figure 3. Frequency of first reports for 24 tree genera since 2000. Note the nativity classification corresponds to the nativity of particular host species, not the genus as a whole.
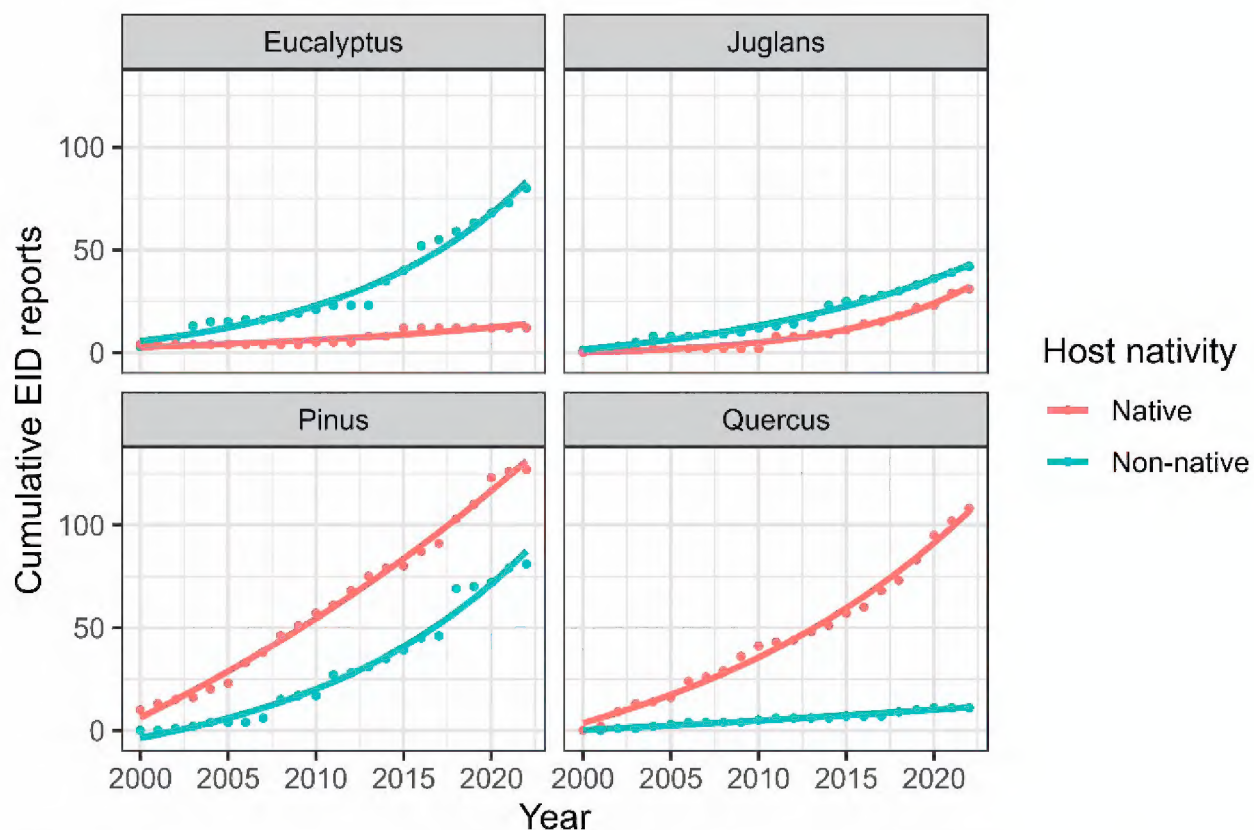
Figure 4. Temporal accumulation of first reports of tree EIDs since 2000 for four host genera with the greatest total number of EID reports in the dataset. Note the nativity classification corresponds to the nativity of particular host species, not the genus as a whole. Models were fitted as y ~ a × exp(b × x) + c, where y is the cumulative number of new reports and x is the number of years elapsed since 2000 (the first year of data collection). To facilitate interpretation and visualisation, x was back-transformed to year (by adding 2000). See also Suppl. material 1: fig. S4.

begun to converge in recent years (Suppl. material 1: fig. S4). *Eucalyptus* showed the opposite pattern, whereby pathogen accumulation is more rapid where it is planted outside its native range. *Eucalyptus* has a relatively narrow native range in Australasia, but has been planted in hundreds of countries abroad, exposing it to a broad range of new pathogens not present in Australasia (Burgess and Wingfield 2017).

Discussion

As has been found for non-native species accumulation (Seebens et al. 2017) and non-native pests specifically (Aukema et al. 2010; Santini et al. 2013), there is little evidence of saturation in emergent tree disease accumulation globally. This is particularly worrisome for native plant populations as EIDs can lead to reduced growth, population reduction and, in severe cases, extirpation. Emergent disease on non-native plants present their own sorts of risk – not only could emergent disease on non-native plants spill over to native plants, as can happen when pathogens track their hosts to a new region, but hosts may then present a sort of biological pathway to the native range (Gougherty and Davies 2022b). For instance, the introduction of white pine blister rust into North America is believed to have been due to the importation of infected native white pines grown in Europe, where they are non-native (Hummer 2000). EIDs on non-native trees, thus, have the potential of being important bellwethers of future threats to trees in their native ranges.

The continued accumulation of EIDs implies diseases are likely to continue to spread and accumulate on new hosts – increasing the likelihood of severe outbreaks and host mortality. The increase in EID reports over the past several decades is likely due to a combination of increased global connectivity and increased reporting (Suppl. material 1: fig. S1). While national and international policies can and have been implemented to limit the spread of plant pathogens across borders (Santini et al. 2018) – this only prevents one type of EID (i.e. those due to introduced pathogens). Even with complete exclusion of non-native pathogens, tree disease can still emerge from shifts in virulence or host range of native pathogens or changing environmental or climatic conditions increasing the opportunity or severity of host-pathogen interactions. Some recent work, for instance, suggests moisture and precipitation may contribute to recent pathogen outbreaks in plants (Romero et al. 2022) (but see Bebber 2022). Changes in climate could also shift the balance between host resistance and pathogen virulence (as predicted by the thermal mismatch hypothesis seen in wildlife species (Cohen et al. 2020)), leading to greater risk of disease outbreak amongst hosts and pathogens that have historically interacted. Understanding the link between environmental change and host-pathogen interactions may help identify the drivers of disease emergence which could improve monitoring and surveillance.

EID accumulation was not equally distributed amongst the genera assessed in this study. *Pinus* had the greatest number of accumulated EIDs – more than double that of any other genus assessed, except *Quercus*. The large number of EIDs on pines is likely

largely attributable to its large geographic range throughout the Northern Hemisphere and its use in forestry around the Globe. While *Quercus* has a similarly large distribution that spans much of the temperate region in the Northern Hemisphere, *Quercus* is also one of the most speciose plant genera (Global Tree Search lists 415 *Quercus* species globally (Beech et al. 2017)), which likely contributes to its large number of accumulated EIDs. The phylogenetic signal in many pests host ranges (Gougherty and Davies 2022b) suggests species-rich genera may be particularly sensitive to accumulating new diseases, as new pathogens may be able to easily jump amongst co-occurring congeners. *Eucalyptus* similarly has a large number of species (Global Tree Search: 723 species), but includes some of the most widely used trees in forestry and occurs in many countries as a non-native species. While it is unclear if hosts accumulate EIDs in similar ways to other pests (Dai et al. 2017), future work identifying the host traits associated with EID accumulation could help improve predictive pest association models and identifying hosts that may be most vulnerable to future EID threats.

Ash dieback

Many of the issues emblematic of EIDs are evident in the close examination of individual pathogens currently spreading on the landscape and encountering new hosts. The pathogen associated with ash dieback, for instance, one of the most frequently included in the dataset, highlights the impacts, challenges and future threats posed by EIDs. Over the past three decades, *Hymenoscyphus fraxineus* (anamorph: *Chalara fraxinea*) has spread rapidly throughout Europe, causing extensive mortality to its main host genus, *Fraxinus*. First reported in Poland in 1992 (Fig. 5) (Kowalski 2006), its ability to spread quickly from airborne spores (estimated at 30–70 km/yr) (Enderle et al. 2019) and human movement of infected plant material, the pathogen reached Spain in 2021 (Stroheker et al. 2021) and is now reported from at least 30 European countries. By the time the pathogen was scientifically described in 2006, it had already appeared and established in many European countries, challenging the implementation of potential eradication or management plans (Skovsgaard et al. 2017). Further, future shifts in the climate spaces used by the ash dieback pathogen and its European hosts introduce new uncertainty into where forests may be most impacted by the pathogen (Goberville et al. 2016). The ability of *H. fraxineus* to infect other, non-native trees – particularly those native to North America, but planted abroad (Drenkhan and Hanso 2010) – highlights another dimension of its potential future impact. An introduction into North America could be particularly damaging as *Fraxinus* there are already experiencing extensive mortality from the emerald ash borer (Herms and McCullough 2014). While the ultimate effect of ash dieback on *Fraxinus* in Europe is uncertain, as some trees appear resistant to the pathogen (McKinney et al. 2014), when placed in a broader context, the epidemic is only one of the latest in a series that shows little sign of slowing. As EIDs continue to accumulate, over time, new high impact, unexpected pathogens are likely to emerge that will devastate host populations and reshape forests – a sequence of events that has repeated in forests around the globe.
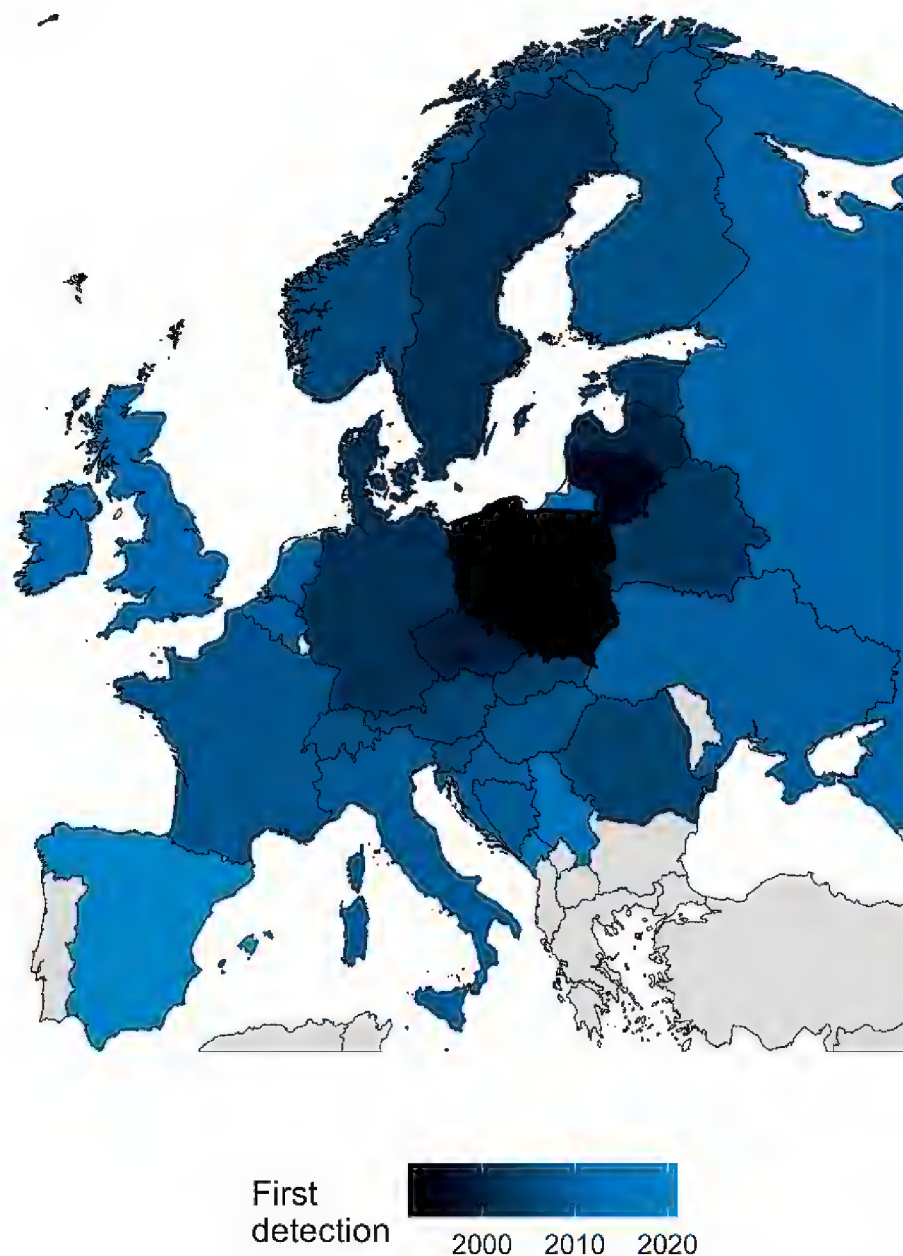
Figure 5. Years of first detection of ash dieback in Europe. Dates were compiled from multiple sources (Timmermann et al. 2011; Keča et al. 2017; Milenković et al. 2017; Orton et al. 2018; CABI 2023).

Limitations

Despite searching thousands of records in the published literature, the estimates here of new disease emergences are certainly underestimated and this is likely for multiple reasons. First, recent work has consistently shown that pest documentations are strongly impacted by country wealth and scientific reporting (Gougherty and Davies 2022a). In line with this expectation, the accumulated number of EID reports increased linearly with the accumulated number of agricultural and biological documents in scientific literature (Suppl. material 1: fig. S1). While many of the host genera assessed here are native to relatively wealthy regions with well-developed reporting systems, non-native ranges extend to all global regions, including less-wealthy countries that may not be well represented in the English-language scientific literature. This could partially explain why EID accumulation tended to be lower in regions where trees were non-native. Furthermore, there is likely an impact-bias in the published records – that is, it is more likely that high-impact pathogens (i.e. those causing severe tree damage) will be investigated and ultimately included in a scientific report (Aukema et al. 2010). Host jumps or pathogen emergence in new geographic regions are likely to go unnoticed if

they cause minimal impact to their hosts. Likewise, many of the records assessed here were first observed in high-visibility locations, such as cities, universities and forest plantations. EIDs in wildlands not easily or frequently visited by the public or scientists are much more likely to go unnoticed for extended periods of time. While the true rate of global EID accumulation may never be known, these results suggest EIDs will continue to threaten natural and managed trees around the Globe in the coming decades.

Conclusion

Emerging infectious diseases pose a major threat to natural and planted trees around the Globe and are acting to reshape forests in the Anthropocene. EIDs are accumulating rapidly on Holarctic trees in both their native and non-native ranges, due to a combination of pathogen and tree introductions and environmental change. Although the rates of accumulation vary regionally and by host species, global trends show little sign of slowing, suggesting the impact of EIDs are likely to continue to compound and threaten tree populations globally.

References

Aguayo J, Elegbede F, Husson C, Saintonge F-X, Marçais B (2014) Modeling climate impact on an emerging disease, the *Phytophthora alni*-induced alder decline. Global Change Biology 20(10): 3209–3221. https://doi.org/10.1111/gcb.12601

Anderson PK, Cunningham AA, Patel NG, Morales FJ, Epstein PR, Daszak P (2004) Emerging infectious diseases of plants: Pathogen pollution, climate change and agrotechnology drivers. Trends in Ecology & Evolution 19(10): 535–544. https://doi.org/10.1016/j.tree.2004.07.021

Arel-Bundock V, Enevoldsen N, Yetman C (2018) countrycode: An R package to convert country names and country codes. Journal of Open Source Software 3(28): e848. https://doi.org/10.21105/joss.00848

Aukema JE, McCullough DG, Von Holle B, Liebhold AM, Britton K, Frankel SJ (2010) Historical accumulation of nonindigenous forest pests in the continental United States. Bioscience 60(11): 886–897. https://doi.org/10.1525/bio.2010.60.11.5

Bebber DP (2022) Weather does influence fungal and oomycete crop disease outbreaks, but ProMED-mail reports don't prove it. The New Phytologist 234(5): 1557–1558. https://doi.org/10.1111/nph.18101

Beech E, Rivers M, Oldfield S, Smith PP (2017) GlobalTreeSearch: The first complete global database of tree species and country distributions. Journal of Sustainable Forestry 36(5): 454–489. https://doi.org/10.1080/10549811.2017.1310049

Bonnamour A, Blake RE, Liebhold AM, Nahrung HF, Roques A, Turner RM, Yamanaka T, Bertelsmeier C (2023) Historical plant introductions predict current insect invasions. Proceedings of the National Academy of Sciences of the United States of America 120(24): e2221826120. https://doi.org/10.1073/pnas.2221826120

Bulman LS, Bradshaw RE, Fraser S, Martín-García J, Barnes I, Musolin DL, La Porta N, Woods AJ, Diez JJ, Koltay A, Drenkhan R, Ahumada R, Poljakovic-Pajnik L, Queloz V, Piškur B, Doğmuş-Lehtijärvi HT, Chira D, Tomešová-Haataja V, Georgieva M, Jankovský L, Anselmi N, Markovskaja S, Papazova-Anakieva I, Sotirovski K, Lazarević J, Adamčíková K, Boroń P, Bragança H, Vettraino AM, Selikhovkin AV, Bulgakov TS, Tubby K (2016) A worldwide perspective on the management and control of *Dothistroma* needle blight. Forest Pathology 46(5): 472–488. https://doi.org/10.1111/efp.12305

Burgess TI, Wingfield MJ (2017) Pathogens on the move: A 100-year global experiment with planted eucalypts. Bioscience 67(1): 14–25. https://doi.org/10.1093/biosci/biw146

Burgess TI, Scott JK, Mcdougall KL, Stukely MJC, Crane C, Dunstan WA, Brigg F, Andjic V, White D, Rudman T, Arentz F, Ota N, Hardy GESJ (2017) Current and projected global distribution of *Phytophthora cinnamomi*, one of the world's worst plant pathogens. Global Change Biology 23(4): 1661–1674. https://doi.org/10.1111/gcb.13492

CABI (2023) Crop Protection Compendium. CAB International. Wallingford.

Chamberlain SA, Boettiger C (2017) R Python, and Ruby clients for GBIF species occurrence data. PeerJ Preprints. https://doi.org/10.7287/peerj.preprints.3304v1

Cohen JM, Sauer EL, Santiago O, Spencer S, Rohr JR (2020) Divergent impacts of warming weather on wildlife disease risk across climates. Science 370: eabb1702. https://doi.org/10.1126/science.abb1702

Contreras-Cornejo HA, Larsen J, Fernández-Pavía SP, Oyama K (2023) Climate change, a booster of disease outbreaks by the plant pathogen *Phytophthora* in oak forests. Rhizosphere 27: e100719. https://doi.org/10.1016/j.rhisph.2023.100719

Corredor-Moreno P, Saunders DGO (2020) Expecting the unexpected: Factors influencing the emergence of fungal and oomycete plant pathogens. The New Phytologist 225(1): 118–125. https://doi.org/10.1111/nph.16007

Dai X, Zhang W, Xu J, Duffy KJ, Guo Q (2017) Global pattern of plant utilization across different organisms: Does plant apparency or plant phylogeny matter? Ecology and Evolution 7(8): 2535–2545. https://doi.org/10.1002/ece3.2882

Drenkhan R, Hanso M (2010) New host species for *Chalara fraxinea*. New Disease Reports 22(1): 16–16. https://doi.org/10.5197/j.2044-0588.2010.022.016

Dudney J, Willing CE, Das AJ, Latimer AM, Nesmith JCB, Battles JJ (2021) Nonlinear shifts in infectious rust disease due to climate change. Nature Communications 12(1): e5102. https://doi.org/10.1038/s41467-021-25182-6

Enderle R, Stenlid J, Vasaitis R (2019) An overview of ash (*Fraxinus* spp.) and the ash dieback disease in Europe. Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources 2019: 1–12. https://doi.org/10.1079/PAVSNNR201914025

Futai K (2021) Pine Wilt Disease and the Decline of Pine Forests: A Global Issue. Cambridge Scholars Publishing, 204 pp.

Ghelardini L, Pepori AL, Luchi N, Capretti P, Santini A (2016) Drivers of emerging fungal diseases of forest trees. Forest Ecology and Management 381: 235–246. https://doi.org/10.1016/j.foreco.2016.09.032

Ghelardini L, Luchi N, Pecori F, Pepori AL, Danti R, Della Rocca G, Capretti P, Tsopelas P, Santini A (2017) Ecology of invasive forest pathogens. Biological Invasions 19(11): 3183–3200. https://doi.org/10.1007/s10530-017-1487-0

Goberville E, Hautekèete N-C, Kirby RR, Piquot Y, Luczak C, Beaugrand G (2016) Climate change and the ash dieback crisis. Scientific Reports 6(1): e35303. https://doi.org/10.1038/srep35303

Gougherty AV, Davies TJ (2022a) A global analysis of tree pests and emerging pest threats. Proceedings of the National Academy of Sciences of the United States of America 119(13): e2113298119. https://doi.org/10.1073/pnas.2113298119

Gougherty AV, Davies TJ (2022b) Host phylogenetic diversity predicts the global extent and composition of tree pests. Ecology Letters 25(1): 101–112. https://doi.org/10.1111/ele.13908

Grünwald NJ, Garbelotto M, Goss EM, Heungens K, Prospero S (2012) Emergence of the sudden oak death pathogen *Phytophthora ramorum*. Trends in Microbiology 20(3): 131–138. https://doi.org/10.1016/j.tim.2011.12.006

Herms DA, McCullough DG (2014) Emerald ash borer invasion of North America: History, biology, ecology, impacts, and management. Annual Review of Entomology 59(1): 13–30. https://doi.org/10.1146/annurev-ento-011613-162051

Hummer KE (2000) History of the origin and dispersal of white pine blister rust. HortTechnology 10(3): 515–517. https://doi.org/10.21273/HORTTECH.10.3.515

Keča N, Kirisits T, Menkis A (2017) First report of the invasive ash dieback pathogen *Hymenoscyphus fraxineus* on *Fraxinus excelsior* and *F. angustifolia* in Serbia. Baltic Forestry 23: 56–59.

Kolb TE, Fettig CJ, Ayres MP, Bentz BJ, Hicke JA, Mathiasen R, Stewart JE, Weed AS (2016) Observed and anticipated impacts of drought on forest insects and diseases in the United States. Forest Ecology and Management 380: 321–334. https://doi.org/10.1016/j.foreco.2016.04.051

Kowalski T (2006) *Chalara fraxinea* sp. nov. associated with dieback of ash (*Fraxinus excelsior*) in Poland. Forest Pathology 36(4): 264–270. https://doi.org/10.1111/j.1439-0329.2006.00453.x

Lenzner B, Latombe G, Schertler A, Seebens H, Yang Q, Winter M, Weigelt P, van Kleunen M, Pyšek P, Pergl J, Kreft H, Dawson W, Dullinger S, Essl F (2022) Naturalized alien floras still carry the legacy of European colonialism. Nature Ecology & Evolution 6(11): 1–10. https://doi.org/10.1038/s41559-022-01865-1

Loo JA (2009) Ecological impacts of non-indigenous invasive fungi as forest pathogens. In: Langor DW, Sweeney J (Eds) Ecological Impacts of Non-Native Invertebrates and Fungi on Terrestrial Ecosystems. Springer Netherlands, Dordrecht, 81–96. https://doi.org/10.1007/978-1-4020-9680-8_6

McCormick JF, Platt RB (1980) Recovery of an Appalachian forest following the chestnut blight or Catherine Keever-You were right! American Midland Naturalist 104(2): 264–273. https://doi.org/10.2307/2424865

McKinney LV, Nielsen LR, Collinge DB, Thomsen IM, Hansen JK, Kjær ED (2014) The ash dieback crisis: Genetic variation in resistance can prove a long-term solution. Plant Pathology 63(3): 485–499. https://doi.org/10.1111/ppa.12196

Milenković I, Jung T, Stanivuković Z, Karadžić D (2017) First report of *Hymenoscyphus fraxineus* on *Fraxinus excelsior* in Montenegro. Forest Pathology 47(5): e12359. https://doi.org/10.1111/efp.12359

Onofri A (2020) The broken bridge between biologists and statisticians: a blog and R package. https://github.com/OnofriAndreaPG/aomisc

Orton ES, Brasier CM, Bilham LJ, Bansal A, Webber JF, Brown JK (2018) Population structure of the ash dieback pathogen, *Hymenoscyphus fraxineus*, in relation to its mode of arrival in the UK. Plant Pathology 67(2): 255–264. https://doi.org/10.1111/ppa.12762

R Core Team (2023) R: A language and environment for statistical computing. Austria. https://www.R-project.org/

Rahmstorf S, Coumou D (2011) Increase of extreme events in a warming world. Proceedings of the National Academy of Sciences of the United States of America 108(44): 17905–17909. https://doi.org/10.1073/pnas.1101766108

Ristaino JB, Anderson PK, Bebber DP, Brauman KA, Cunniffe NJ, Fedoroff NV, Finegold C, Garrett KA, Gilligan CA, Jones CM, Martin MD, MacDonald GK, Neenan P, Records A, Schmale DG, Tateosian L, Wei Q (2021) The persistent threat of emerging plant disease pandemics to global food security. Proceedings of the National Academy of Sciences of the United States of America 118(23): e2022239118. https://doi.org/10.1073/pnas.2022239118

Romero F, Cazzato S, Walder F, Vogelgsang S, Bender SF, van der Heijden MGA (2022) Humidity and high temperature are important for predicting fungal disease outbreaks worldwide. The New Phytologist 234(5): 1553–1556. https://doi.org/10.1111/nph.17340

Rosenzweig C, Iglesius A, Yang XB, Epstein PR, Chivian E (2001) Climate change and extreme weather events – Implications for food production, plant diseases, and pests. Global Change & Human Health 2(2): 90–104. https://doi.org/10.1023/A:1015086831467

Santini A, Ghelardini L, Pace CD, Desprez-Loustau ML, Capretti P, Chandelier A, Cech T, Chira D, Diamandis S, Gaitniekis T, Hantula J, Holdenrieder O, Jankovsky L, Jung T, Jurc D, Kirisits T, Kunca A, Lygis V, Malecka M, Marcais B, Schmitz S, Schumacher J, Solheim H, Solla A, Szabò I, Tsopelas P, Vannini A, Vettraino AM, Webber J, Woodward S, Stenlid J (2013) Biogeographical patterns and determinants of invasion by forest pathogens in Europe. The New Phytologist 197(1): 238–250. https://doi.org/10.1111/j.1469-8137.2012.04364.x

Santini A, Liebhold A, Migliorini D, Woodward S (2018) Tracing the role of human civilization in the globalization of plant pathogens. The ISME Journal 12(3): 647–652. https://doi.org/10.1038/s41396-017-0013-9

SCImago (2022) SJR – SCImago Journal & Country Rank. https://www.scimagojr.com/ [Accessed July 12, 2022]

Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE, Jeschke JM, Pagad S, Pyšek P, Winter M, Arianoutsou M, Bacher S, Blasius B, Brundu G, Capinha C, Celesti-Grapow L, Dawson W, Dullinger S, Fuentes N, Jäger H, Kartesz J, Kenis M, Kreft H, Kühn I, Lenzner B, Liebhold A, Mosena A, Moser D, Nishino M, Pearman D, Pergl J, Rabitsch W, Rojas-Sandoval J, Roques A, Rorke S, Rossinelli S, Roy HE, Scalera R, Schindler S, Štajerová K, Tokarska-Guzik B, van Kleunen M, Walker K, Weigelt P, Yamanaka T, Essl F (2017) No saturation in the accumulation of alien species worldwide. Nature Communications 8(1): e14435. https://doi.org/10.1038/ncomms14435

Skovsgaard JP, Wilhelm GJ, Thomsen IM, Metzler B, Kirisits T, Havrdová L, Enderle R, Dobrowolska D, Cleary M, Clark J (2017) Silvicultural strategies for *Fraxinus excelsior* in

response to dieback caused by *Hymenoscyphus fraxineus*. Forestry. Forestry 90(4): 455–472. https://doi.org/10.1093/forestry/cpx012

Smith GR, Fletcher JD, Marroni V, Kean JM, Stringer LD, Vereijssen J (2017) Plant pathogen eradication: Determinants of successful programs. Australasian Plant Pathology 46(3): 277–284. https://doi.org/10.1007/s13313-017-0489-9

Stroheker S, Queloz V, Nemesio-Gorriz M (2021) First report of *Hymenoscyphus fraxineus* causing ash dieback in Spain. New Disease Reports 44(2): e12054. https://doi.org/10.1002/ndr2.12054

Timmermann V, Børja I, Hietala AM, Kirisits T, Solheim H (2011) Ash dieback: Pathogen spread and diurnal patterns of ascospore dispersal, with special emphasis on Norway*. Bulletin OEPP. EPPO Bulletin. European and Mediterranean Plant Protection Organisation 41(1): 14–20. https://doi.org/10.1111/j.1365-2338.2010.02429.x

Tomoshevich M, Kirichenko N, Holmes K, Kenis M (2013) Foliar fungal pathogens of European woody plants in Siberia: An early warning of potential threats? Forest Pathology 43: 345–359. https://doi.org/10.1111/efp.12036

van der Nest A, Wingfield MJ, Janoušek J, Barnes I (2019) Lecanosticta acicola: A growing threat to expanding global pine forests and plantations. Molecular Plant Pathology 20(10): 1327–1364. https://doi.org/10.1111/mpp.12853

Woods A, Coates KD, Hamann A (2005) Is an unprecedented *Dothistroma* Needle Blight epidemic related to climate change? Bioscience 55(9): 761–769. https://doi.org/10.1641/0006-3568(2005)055[0761:IAUDNB]2.0.CO;2

Supplementary material 1

Supplementary images
Author: Andrew V. Gougherty
Data type: docx
Explanation note: **fig. S1.** Relationship between the cumulative number of all citable scientific documents in the agricultural (ag.) and biological (biol.) literature and the cumulative number of EID reports. **fig. S2.** Proportion of all EID reports published in "Plant Disease" represented by Holarctic trees, used in this study. **fig. S3.** Temporal accumulation of first reports of tree EIDs since 2000 for four geographic regions and 24 tree genera. **fig. S4.** Temporal accumulation of first reports of tree EIDs since 2000 for four host genera with the greatest total number of EID reports in the dataset.
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Link: https://doi.org/10.3897/neobiota.87.103525.suppl1

Supplementary material 2

Publications of first reports of pathogens on 24 tree host genera published since 2000

Author: Andrew V. Gougherty

Data type: xlsx

Explanation note: Note the host species name may not match the host species name in the article if it did not match the GBIF taxonomic backbone.

Link: https://doi.org/10.3897/neobiota.87.103525.suppl2

Supplementary material 3

Parameters estimates of an exponential model fit to the accumulation of new disease reports for various geographic, host, and nativity subsets

Author: Andrew V. Gougherty

Data type: xlsx

Explanation note: Models were fit as $y \sim a \times \exp(b \times x) + c$, where y is the cumulative number of new reports, and x is the number of years elapsed since 2000 (the first year of data collection).

Link: https://doi.org/10.3897/neobiota.87.103525.suppl3